Department of Ecology, Ethology and Evolution,
University of Illinois, Urbana

Mustelid Spacing Patterns:
Variations on a Theme by *Mustela*

By Roger A. Powell

With one figure

Abstract

This is a review of mustelid spacing patterns. The Mustelinae appear to have intra-sexual territories where ♂♂ are territorial against ♂♂, ♀♀ against ♀♀, but there is extensive territory overlap between sexes. Mustelids of other subfamilies appear to have variations on this theme; usually female territories are replaced by territories of family groups of one adult ♀ and her most recent offspring. Sea otters and European badgers do not appear to fit into these organizational schemes.

There is a strong correlation between degree of intrasexual territoriality, sexual dimorphism in body size, degree of body elongation and degree of carnivory. It is suggested that energy requirements of individuals may tie these correlations together.

LOCKIE stated in 1966 that a review of territory and home range in small carnivores was easy because the literature was so meager. During the past dozen years, elucidating reports have been published on spacing patterns of least weasels (*Mustela nivalis*), stoats (*M. erminea*) and otters (*Lutra lutra*), mostly from Great Britain and Sweden. In addition, a good deal of suggestive information has been published on other mustelids. Therefore, I here review what is now known about mustelid spacing patterns as a guide for future research.

In a general way, the spacing patterns of a population can be summarized as a set of ordered relationships between individuals or groups of individuals. For the Mustelidae, there are two major levels from which organization can be viewed. On the population level, ordered patterns of relationships exist between solitary individuals and/or groups of individuals. On the individual level, mustelids are either solitary or found in small groups. For all mustelids studied, three classes of individuals exist: transients, temporary residents and residents. Precise definition of these classes is difficult but the names are generally descriptive: transients are individuals who merely pass through an

area, temporary residents stay for a short time, and residents stay for extended periods or for the duration of their lives.

The terms home range and territory are generally understood, although each has been subject to various interpretations (VERNER 1977). Home range is the area covered by an animal in its normal day to day activities; territory is an area from which conspecifics are excluded, an area of exclusive use or an area with priority access to resources (BURT 1943; EWER 1973). However, as EWER (1973) pointed out, the way we define home range and territory in practice involves an external analysis of what other animals are doing. Our perception of what animals do is certainly different than what those animals themselves perceive. Therefore we should not expect permanent, clearly defined patterns to exist. As a functional definition, I define territory as an area of exclusive use. This implies priority access to resources and may imply defense (by aggression or by marking).

The Basic Theme

A basic spacing pattern for the Mustelidae can be seen in the genera *Mustela* and *Martes*. On the individual level, members of these genera are solitary except for reproductive purposes. On the population level, there appears to be a well structured pattern of spacing between individuals. CLARK and CAMPBELL (unpubl.), ERLINGE (1974, 1977a), HAWLEY and NEWBY (1957), KING (1975), LOCKIE (1966) and MOORS (1975) have all found similar patterns of spacing for American marten (*Martes americana*), least weasels and stoats. Given adequate food and proper habitat, members of these species have intra-sexual territories during at least part of the year: ♂ ♂ are territorial against ♂ ♂, ♀♀ against ♀♀, but the territory of a member of one sex may overlap the territory of a member of the other sex. Environment and sexual condition may affect territoriality (ERLINGE 1974, 1977a; KING 1975; LOCKIE 1966; MOORS 1975).

HAWLEY and NEWBY (1957) were the first to report intrasexual territoriality. By live-trapping martens in Glacier National Park they were able to obtain reasonable data on the home ranges of many individuals. Home ranges of adult martens of like sex "were rather evenly distributed with little overlap", while martens of opposite sex appeared "quite tolerant of each other". Although HAWLEY and NEWBY did not observe territorial defense by any individuals in their population, they did note "anti-social" behavior between two martens when they caught sight of each other in the wild. The two martens growled and avoided close approaches to each other. Probably of more importance, HAWLEY and NEWBY noted that when an adult marten disappeared the territories of adjacent martens of the same sex were extended into the vacated area. Transients and temporary residents did not affect the spacing pattern of residents.

CLARK and CAMPBELL (unpubl.) reported similar spacing patterns for martens from a live-trapping study during 1975 and 1976 in Grand Teton National Park and Teton National Forest. Again adult ♂ ♂ had areas of exclusive use, suggesting intrasexual territoriality. In contrast to the results of HAWLEY and NEWBY (1957), CLARK and CAMPBELL found extensive overlap of female ranges. Unfortunately, CLARK and CAMPBELL do not state the ages of the ♀♀ and the reported data cover only short time periods during the two years. Extensive overlap of male and female home ranges suggested tolerance between the sexes.

MECH and ROGERS (1977) presented limited data which do not contradict an intrasexual territorial spacing pattern for martens in Minnesota.

LOCKIE (1966) reported a similar pattern of spacing for least weasels and stoats. Again the organization was deduced from live-trapping results but the data appear even more extensive than those of HAWLEY and NEWBY (1957). Male least weasels exhibited nearly non-overlapping home ranges during winter; during summer the overlap increased but clear areas of exclusive use were maintained. Within the male home ranges, female least weasels occupied much smaller home ranges which were seldom contiguous but used exclusively by the resident ♀. Transients and temporary residents were not uncommon but did not appear to affect the spacing pattern of the residents.

The stoats studied by LOCKIE (1966) showed the same pattern of organization as the least weasels but the data are more sparse due to the large home ranges of individual stoats.

ERLINGE (1974), KING (1975) and MOORS (1975) have recently reported on spacing patterns of least weasels determined by live-trapping and ERLINGE (1977a) has reported on spacing patterns of stoats determined by live-trapping, tracking and radio-telemetry. In all of these studies the same pattern appears: intrasexual territories with overlap of the territories of the opposite sex. In addition, a better understanding of the stability and maintenance of the territories has been reached.

Although the territories of male and female least weasels and stoats overlap, a ♀ appears to restrict the use of her territory by the resident ♂. During times other than the breeding season, a ♂ seldom enters a ♀'s territory (ERLINGE 1974, 1977a), even though the ♀'s territory may lie completely within his own territory. When a ♂ does enter a ♀'s territory, the two use different parts of that territory (ERLINGE 1974).

Spatio-temporal separation also exists between male least weasels in the regions of home range overlap (KING 1975). KING never found two resident ♂♂ occupying the region of home range overlap at the same time.

Territories of least weasels and stoats are maintained by scent marking and by dominance relationships (ERLINGE 1974, 1977a, 1977b). ERLINGE found that resident least weasels and stoats of all sex-age classes were dominant to introduced members of the same sex-age class. Adult male stoats, however, were dominant to resident members of all other sex-age classes except sometimes pregnant or oestrous ♀♀. ERLINGE functionally defined a dominant stoat as a stoat which displayed at least one of several behaviors taken as criteria for dominance: "approach causing submissive vocalization of the animal being visited, thrust and threat vocalization causing fleeing and escape, occupation of nest, robbery of prey, and chase".

Other studies imply that dominance relationships affect territory maintenance in American martens and the three North American and European weasel species. WECKWERTH and HAWLEY (1962) found that when the food supply decreased, female martens of all ages and juvenile male martens fared poorly compared to resident adult ♂♂. Adult ♀♀ lost more weight than adult ♂♂ and had a higher mortality rate. LOCKIE (1966) found that during a period of food shortage and erratic fluctuations of vole populations, female least weasels completely disappeared from his study area. I found during a removal study in Upper Peninsula Michigan and Minnesota (POWELL 1978) that resident male long-tailed weasels (*Mustela frenata*) and stoats were captured before resident ♀♀. I also found that long-tailed weasels were captured before stoats, indicating that there may be a dominance relationship between species as well as within each species.

Although LOCKIE (1966) and HAWLEY and NEWBY (1957) found that territories were maintained during all seasons of the year, more recent work has shown that territoriality may break down under certain conditions. The most important factors affecting territory maintenance are food, habitat and sexual activity.

WATSON and MOSS (1970) concluded that least weasel territoriality was not affected by food supply but other studies contradict this conclusion. ERLINGE (1974), KING (1975) and MOORS (1975) all found that the spacing patterns of their least weasels and stoats were affected by food supply but the spatial changes were not predictable. LOCKIE (1966) felt that a minimum density of least weasels and stoats was necessary for members of these species to maintain territories or distinct home ranges; their densities were, in turn, dependent on prey densities. ERLINGE (1974) showed, however, that least weasels may maintain non-contiguous, distinct home ranges if vole populations decrease and cause least weasel populations to fall very low. Nonetheless a minimum supply of food appears necessary for territoriality to exist among least weasels (ERLINGE 1974) and stoats and this minimum food supply varies with habitat (KING 1975). Thus, a larger food supply is necessary in areas with less cover (KING 1975) and a comparatively stable but low food supply may allow weasel species to set up a territorial pattern whereas a large but more variable food supply may not (KING 1975). This is consistent with LOCKIE's (1966) observation that the stable territorial pattern disintegrated when the vole population crashed and failed to re-establish as long as the vole population size was erratic. ERLINGE (1977a), KING (1975) and MOORS (1975) found that least weasels and stoats totally avoid certain habitats; these habitats usually lack food *and* cover. MOORS (1975) found that least weasels never ventured far from stone walls in his Scottish farmland study and therefore his weasels' territories were linear in nature.

During the breeding season (late spring and summer, depending on the species) male least weasels and stoats travel widely and there is much home range overlap (ERLINGE 1974, 1977a; LOCKIE 1966; MOORS 1975). ♀♀, however, appear to maintain well-defined territories during this period (ERLINGE 1974, 1977a). The movements of ♂♂ appear to be related to breeding and territory defense (ERLINGE 1977a). By late summer, well defined territories are again established (ERLINGE 1974, 1977a; MOORS 1975) and during autumn, juvenile ♂♂ and ♀♀ settle down in areas close to their area of birth (ERLINGE 1977a). A fairly stable spacing pattern exists during winter, and the following spring juvenile ♀♀ and ♂♂ maintain territories as do adults (ERLINGE 1977a).

From the limited data available, I have been able to find several other mustelids that appear to have intrasexual territoriality.

GERELL (1970) studied feral ranch minks (*Mustela vison*) in southern Sweden. Because the minks did not venture far from water courses, he expressed home ranges as length of stream bank or lake shore. In one of two areas studied, GERELL radio-tracked two adult ♂♂, one juvenile ♂ and one adult ♀ and live-trapped three additional juvenile ♀♀. The spacing pattern which appeared is almost exactly like that found in least weasels and stoats. The adult and juvenile ♂♂ occupied exclusive lengths of stream bank much as MOORS' (1975) weasels occupied the area along stone walls. The ♀ occupied a stream bank contained within the territory of one of the adult ♂♂. The juvenile ♀♀ were trapped within the territory of the same adult ♂ as contained the territory of the adult ♀ but the juveniles were never trapped within the adult ♀'s territory. As with least weasels and stoats, juvenile ♀♀ tended to take up residence close to their birthplace as they dispersed but juvenile ♂♂ ap-

peared to be forced into peripheral areas not occupied by adult ♂♂. GERELL also found that the territorial patterns became less clear during the mating season as male minks travelled long distances and did not remain within their formerly established territories. Territories are apparently maintained by marking (BRINCK et al. 1978).

In his Iowa marshes, ERRINGTON (1943) found even spacing of female minks with young and believed that each ♀ had exclusive use of her home range. He implies similar spacing for ♂♂. MECH (1965) states that male minks will mate with more than one ♀, suggesting that more than one ♀ will reside within the home range of a ♂ or that ♂♂ go beyond their normal territories in the breeding season. This indicates that the behavior and spacing pattern found by GERELL (1970) for feral minks are accurate for native, wild minks.

The little information available on black-footed ferrets (*Mustela nigripes*) is suggestive of intrasexual territoriality. Two adult black-footed ferrets of the same sex have not been observed in the same small prairie dog (*Cynomys* spp.) town (less than 50 acres) or in the same area of a large prairie dog town. Two adults of opposite sex have been found in the same prairie dog town or same part of a large prairie dog town but they were never found in the same places at the same time (HENDERSON et al. 1969; HILLMAN 1968).

KELLY (1977) did not believe that the radio collared fishers (*Martes pennanti*) in his New Hampshire study area exhibited territoriality but he did not analyze his data for intrasexual spacing or over time periods of a few months to allow for home range shifts. The data available in his thesis appear to show that his fishers may have been exhibiting intrasexual territoriality. Although home ranges shifted in time, for any period of a few months home ranges for individuals of the same sex did not overlap by more than one or a very few location points.

The data from my fisher study in Upper Peninsula Michigan are sparse with respect to spacing but they support intrasexual territoriality. Using tracking in the snow augmented by live-trapping and radio-telemetry as my sources of data, I found that individual fishers were strongly solitary. Two fishers would sometimes travel along the same trail for short distances but there was no evidence that they ever met (POWELL 1977). Tracks crossing roads on any one day were widely spaced and fishers appeared to avoid areas utilized by other fishers. Two ♂♂ radio-tracked during winter 1975—76 utilized adjacent and mostly non-overlapping home ranges. One of these ♂♂ occupied the former home range of a ♂ radio-tagged the previous winter and known no longer to be in the area.

In California, BUCK et al. (1978) have also found non-overlapping home ranges of male fishers with female home ranges within those of the ♂♂. In other tracking studies, DEVOS (1952) and COULTER (1966) found that fishers were quite solitary but QUICK (1953) believed that fishers sometimes travelled in groups of two or three.

JENSEN and JENSEN (1972) presented information on beech martens (*Martes foina*) in Denmark. Beech martens sleep and ♀♀ raise their young predominantly in the attics of houses; they forage in the surrounding area. JENSEN and JENSEN state that only one adult uses the attic of a house and that they are solitary except for breeding and raising young. This implies that there is exclusive use of certain areas. Information supplied on European pine martens (*Martes martes*) is limited but JENSEN and JENSEN state that they are solitary in Denmark. Other information on European pine martens, sables (*M. zibellina*) and Japanese martens (*M. melampus*) indicate many similarities of morphology, habits and habitat to the American marten. It is possible that these

four species are really only one circumpolar species (ANDERSON 1970; HAG-MEIER 1955, 1961). It is therefore likely that they all have very similar spacing patterns.

RAUSCH and PEARSON (1972) found that male wolverines (*Gulo gulo*) have much larger home ranges than female wolverines and they imply that members of each sex occupy home ranges exclusive of other members of their sex. KROTT (1959; from EWER 1973) also found that ♂♂ and ♀♀ held territories exclusive of other members of the same sex. KROTT believed that both food supply and denning sites affected territory size.

Two more mustelines are believed to be solitary, the marbled polecat (*Vormela peregusna*) and the zorille (*Ictonyx striatus*) but little more is known of their natural history (WALKER 1968). ROWE-ROWE (1978 a) was able to house pairs of zorilles together during the breeding season, however.

Variations on the Theme

In some mustelids there are variations of the spacing pattern found in mustelines. On the individual level, some members of some species are found in groups while others appear solitary. On the population level, the spacing pattern between groups appears the same as found between individuals in the Mustelinae.

Otters (*Lutra lutra*) introduce an interesting variation on intrasexual territoriality (ERLINGE 1967, 1968). As with mink, otter home ranges are oriented along water courses and are linear in nature. Male otters maintain territories against other male otters and the territories are maintained by scent marking, by a dominance hierarchy among male otters and by aggression. There may be slight overlap of adjacent territories and boundaries shift from time to time. If a male otter disappears, adjacent ♂♂ extend their territories into the vacated area. Each male territory overlaps or includes one or more of the smaller territories maintained by family groups consisting of a ♀ and her young. The territories of family groups overlap little and often are not contiguous. Juvenile and subadult ♂♂ are forced to occupy suboptimal habitats and are excluded from male territories. There appears to be an autumn peak in territorial activity as two year old ♂♂ attempt to set up territories.

Otters can be labelled as transients, temporary residents and residents. Territorial ♂♂ and ♀♀ with family groups are residents. Transients and temporary residents are mainly juveniles and subadults, though adult ♀♀ without family groups may temporarily settle into spaces between family groups and/or travel with resident male otters.

Skunks (*Mephitis mephitis, Spilogale putorius*) appear to exhibit another variation on the territorial theme, though the information is mostly suggestive, especially for spotted skunks. ALLEN (1939), ALLEN and SHAPTON (1942) and HAMILTON (1937) studied winter denning of striped skunks. No more than one male skunk was found in a den, though up to 10 ♀♀ might den together with one ♂. VERTS (1967) found extensive overlap of home ranges but did not analyse his data by sex. WIGHT (1931) reported that ♀♀ will only tolerate the presence of a ♂ during winter or when in breeding condition. It is possible that ♂♂ hold territories while there is some sort of loose-knit organization among ♀♀, perhaps a familial relationship.

WALKER (1968) states that spotted skunks may den in groups and CRABB (1948) found extensive overlap of home ranges. As there is no available in-

formation on spatial organization with respect to sex, this information does not contradict there being the same sort of organization as found in striped skunks.

Possible Exceptions to the Theme

There are at least two mustelids which may be exceptions from having a spacing pattern similar to that of the weasels and martens: sea otters (*Enhydra lutris*) and European badgers (*Meles meles*).

Sea otters live in large groups but tend to segregate by sex (KENYON 1969; SHIMEK and MONK 1977). Individuals stay within a home range which extends over 8—16 km (KENYON 1969) but home ranges of individuals are nearly completely overlapping, especially within the same sex. ♂♂ move into the female occupied areas to interact with ♀♀ and to breed (KENYON 1969; SHIMEK and MONK 1977). KENYON (1969) noted, however, that some ♂♂ would consistently locate themselves on a rock overlooking the female area. When a ♀ passed, the ♂ would swim out to her and court. If she were not receptive the ♂ would return to his rock or to a favorite feeding place. If she were receptive, she would choose a rock in the vicinity where the pair would sleep and groom during the mating period of up to several days. ♂♂ made no attempt to drive other ♂♂ from the vicinity of their observation rocks. Thus, some sort of territorial behavior may exist in male sea otters but the evidence is meager and such a territorial system would be very different from intrasexual territoriality.

European badgers appear to have ♂-♀ pairs as the basic unit of social organization (NEAL 1948) but several badgers, consisting of more than a single pair and their offspring, may occupy a common set of burrows (called a "sett") and have a communal territory (KRUUK 1978a; NEAL 1948). Territories are defended by aggression and by marking (KRUUK 1978a). During winter, badgers den up much as skunks do but more than one pair will often occupy the same sett. During summer when mating occurs there is a good deal of chasing, scuffling and scent marking but this does not affect the structure of the group (NEAL 1948). Badger spacing patterns appear to maximize long-term foraging efficiency for earthworms, the badger's major food (KRUUK 1978b).

The limited information presented in WALKER (1968) suggests tayras (*Eira barbara*), grisons (*Grison* spp.), and African striped weasels (*Poecilogale albinucha*) and ratels (*Mellivora capensis*; also in KRUUK 1978b) as further possible exceptions as all have been seen in pairs or larger groups. KAUFMANN and KAUFMANN (1965) observed a male and female tayra to maintain an amiable relationship well beyond the age at which I had to separate a male and female fisher (POWELL 1977). J. H. KAUFMANN (pers. comm.) has seen female tayras with their young, suggesting that tayras may be a variation on the theme rather than an exception. ROWE-ROWE (1978a) was able to house pairs of African striped weasels during the breeding season.

Correlations

McNAB (1963) was the first to demonstrate the correlation between the size of a mammal and the size of its home range. SCHOENER (1968) further showed that the slope of the curve relating weight of an animal to its home range size changes with feeding strategies. There appear to be correlations

among mustelids between feeding strategy, spacing pattern, sexual dimorphism in body size and degree of elongate shape.

I have gathered data from the literature on weights and body lengths of ♂♂ and ♀♀ of 19 mustelid species (Fig. 1). The information gathered is not complete but shows definite trends. I have chosen as an elongation index for a species the average body length of ♂♂ divided by the cube root of the average weight of ♂♂. The index is little changed by using ♀♀ or both sexes. Because the weight of an animal increases as the cube of equal increases in all three linear dimensions, this index of elongation increases with increased body length. I have chosen average male weight divided by average female weight as an index of sexual dimorphism in body size. The correlation of these two indices has been plotted. The correlation coefficient of the regression is 0.58, which is highly significant (p << 0.005).
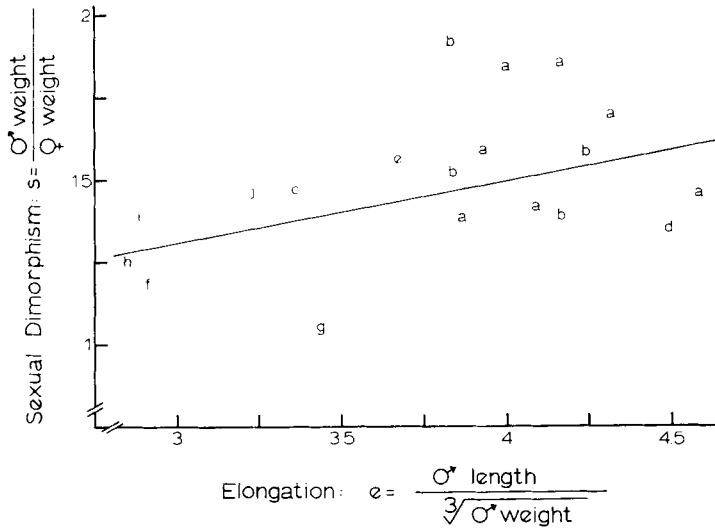

Fig. 1: Correlation between elongation "e" (male length divided by the cube root of male weight) and sexual dimorphism "s" (male weight divided by female weight) for 19 species in the Mustelidae. The equation for the regression is: s = 0.18 e + 0.80 (r = 0.58, p < 0.005). a = *Mustela* spp.: *M. altica, M. erminea, M. frenata, M. nigripes, M. nivalis, M. putorius, M. vison*; b = *Martes* spp.: *M. americana, M. martes, M. pennanti, M. zibellica*; c = *Gulo gulo*; d = *Poecilogale albinucha*; e = *Ictonyx striatus*; f = *Meles meles*; g = *Taxidea taxus*; h = *Mephitis mephitis*; i = *Spilogale putorius*; j = *Lutra lutra*. Sources for the weights and lengths of the species are BURT (1957), BURT and GROSSENHEIDER (1964), CLEM (1977), CLEMENTS (1975), COULTER (1966), CRABB (1944), FORTENBERRY (1972), GRINNELL et al. (1937), GUNDERSON and BEER (1953), HALL (1951), HAMILTON (1933), HAMILTON and COOK (1955), HENDERSON et al. (1969), IRVINE (1961, 1962), JENSEN and JENSEN (1972), KELLY (1977), MECH (per. comm.), NOVIKOV (1956), OGNEV (1931), PALMER (1954), PETERSON (1966), POWELL (1977, unpubl. data), ROWE-ROWE (1978b), SNOW (1972), SOUTHERN (1964), Wisconsin Department of Natural Resources (unpubl. files)

Note in the Figure that those mustelids with elongate bodies and large sexual dimorphism in body size (a, b, c) are mustelines which appear to have clear cut intrasexual territories. They are also the mustelids which are the most carnivorous (having predominantly mammalian and avian prey; EWER 1973; POWELL, unpubl. data) and have the highest metabolic rates (BROWN and LASIEWSKI 1972; MOORS 1975; POWELL 1977, 1979). Otters (j) are further to the lower left than mustelines, show a variation on the intrasexual territory pattern and are less typically carnivorous in that their prey tends to be found in large populations and is ectothermic or invertebrate. Skunks (h, i) are

further yet to the lower left and show an even greater deviation from intra-sexual territoriality. Skunks are also the most omnivorous of the mustelids, with the possible exception of the European badger (f) which is also found in the lower left corner of the graph. It is interesting to note that American badgers (g, *Taxidea taxus*) are more elongate than European badgers and are also more carnivorous (Ewer 1973; Walker 1968). Likewise, spotted skunks (i) are more sexually dimorphic in body size than striped skunks (h) and are more carnivorous (Ewer 1973; Gunderson and Beer 1953; Walker 1968). African striped weasels are more elongate and more carnivorous than zorilles (Rowe-Rowe 1978 a, 1978 b) but zorilles are more sexually dimorphic in body size than the weasels (Rowe-Rowe 1978 b). More information on the spacing patterns of these two species is needed.

KAUFMANN and KAUFMANN (1965) reported on two tropical mustelids: tayras and grisons. Tayras ate much fruit along with small vertebrates and the sexual dimorphism was small (5.9 kg ♂, 4.3 kg ♀; sexual dimorphism index of 1.37). Grisons ate insects, small vertebrates and some fruit and sexual dimorphism was fairly large (3.3 kg ♂, 1.8 kg ♀; sexual dimorphism of 1.80; DALQUIST and ROBERTS 1952).

Thus, those mustelids with the most clear cut intrasexual territoriality are those which are most carnivorous, most elongate and most sexually dimor-phic. It has been suggested that sexual dimorphism in body size together with intrasexual territoriality could be one way of decreasing competition for food so that the resident mustelids might meet their high energetic demands more easily (BROWN and LASIEWSKI 1972). Although this has been given supportive comments in the literature (ERLINGE 1974, 1977a) I have only been able to find five sets of data which are directly applicable for testing. ERLINGE (1974) did find differences in the diets of male and female least weasels in Sweden. COULTER (1966) compared the incidence of different foods in 113 male and 129 female fisher digestive tracts and found no differences (chi square, p > 0.10). CLEM (1977) was also unable to find differences between 117 male and 153 female fisher digestive tracts. Of special interest is that COULTER and CLEM found no differences in the incidences of porcupines (*Erethizon dor-satum*) in the digestive tracts of male and female fishers. Such a difference had been expected from other aspects of COULTER's work and from the work of EARLE (1978) because of the large size of porcupines compared to fishers. KELLY (1977) did find a significant difference in the incidence of porcupine quills in male and female fisher carcasses (p < 0.01) but did not find any sexual differences in digestive tract contents of fishers in New Hampshire. YURGENSON (1947) claimed to have found a sexual difference in the diet of European pine martens but statistical analysis of his results (analysis he did not perform) show that the differences he found were not significant (chi square, p > 0.10).

I have postulated (POWELL 1977, 1979) as have others (MOORS 1975; REYNOLDS 1972) that sexual dimorphism is a product of increased energy expenditure during reproduction. Conflicting selective pressures determine a mustelid's size. Large size enables exploitation of a wider range of prey sizes whereas small size keeps daily energy expenditure low. Female mustelids which raise young with no help from a ♂ are under further selection for small size to reduce energy requirements during gestation, lactation and weaning. An hypothetical female least weasel the size of a ♂ would expend 25 % more energy while raising a litter than would a normal sized ♀. This is approxi-mately equivalent to catching 45 to 55 additional short-tailed voles (*Microtus agrestis*) during that period (MOORS 1975) and probably represents strong

selection for small female size to reduce maintenance energy requirements during reproduction. Thus maximum size for a male mustelid is larger than that for a ♀ of his species.

A corollary to this is that in areas of abundant food, ♂♂ should show an increase in size (because size is no longer limited by nutrition and ♂♂ can approach maximum size) and variability of size (because ♂♂ will not reach full size immediately). ♀♀ should not show such an increase in size because their maximum size is much smaller and more easily attained with more limited food supplies. This is exactly what happened when fishers from Minnesota were released in Upper Peninsula Michigan (POWELL 1977, 1979). 15 years ago, fishers were released into a food supply (porcupines) unexploited by other predators in Michigan (POWELL and BRANDER 1977). Male fishers now average significantly heavier than the male fishers which were originally released (p < 0.01, Student's test; POWELL 1977, 1979) and are heavier than male fishers presently in Minnesota. These differences are not explained by age structure. Female fishers' weights have not changed.

Degree of elongation may be dependent on diet and methods of capturing prey (catching mice and other small mammals down holes) and in turn affects energetics through increased convective heat loss and consequent elevated metabolic rate (BROWN and LASIEWSKI 1972). Energetic affect sexual dimorphism in body size and diet (higher food requirements because of elevated metabolic rate). The causal relationships between spacing patterns and these other variables are unknown.

Thus, energetics appears to explain sexual dimorphism in long, slender mustelids. There are correlations between sexual dimorphism, elongation, carnivory and spacing patterns. I believe that high energy requirements of mustelids and not diet per se will be found to be the key which explains all of the correlations presented here. I urge future workers to take this into consideration while planning research on mustelids.

Summary

The basic mustelid spacing pattern appears to be intrasexual territoriality. This spacing pattern has been documented for least weasels, stoats and American pine martens. There is evidence in the literature that minks, black-footed ferrets, fishers, beech martens and wolverines also exhibit this spacing pattern. Scent marking, dominance relations and food supply affect the maintenance and stability of the spacing pattern.

Otters show a variation on intrasexual territoriality. Territories of adult ♀♀ are shared with their offspring of the year. Some sort of familial variation on intrasexual territoriality may be exhibited by spotted and striped skunks.

Sea otters and European badgers exhibit spacing patterns apparently unrelated to intrasexual territoriality. The spacing pattern of the latter is probably related to foraging efficiency for the species' major prey.

Elongate mustelids tend to show large sexual dimorphism in body size. These species also exhibit intrasexual territoriality and tend to be more carnivorous than those species which are neither elongate nor sexually dimorphic.

Zusammenfassung

Das basale soziale Siedlungs- und Ausbreitungsmuster der Musteliden scheint die Revierabgrenzung gegen gleichgeschlechtliche Artgenossen (intra-sexuelle Territorialität) zu sein. Es ist nachgewiesen für Mauswiesel, Hermelin

und amerikanischen Fichtenmarder, nach der Literatur wahrscheinlich für Nerz, Schwarzfußiltis, Fischmarder, Steinmarder und Vielfraß. Die Beständigkeit dieses Siedlungsmusters wird von Duftmarken, Rangunterschieden und Nahrungsangebot beeinflußt.

Ottern zeigen eine Abwandlung dieses Musters; erwachsene ♀♀ teilen ihr Revier mit ihren diesjährigen Nachkommen. Flecken- und Streifenskunks könnten ähnliche familienbezogene Abwandlungen des Siedlungsmusters haben.

Seeotter und Dachs haben ganz andere Siedlungsmuster. Das des Dachses scheint dem günstigsten Sammeln der Vorzugsbeute angepaßt.

Langgestreckte Musteliden neigen zu stärkerem Geschlechtsunterschied in der Körpergröße. Sie zeigen das basale Muster und sind deutlicher carnivor als die weder langgestreckten noch sexualdimorphen Arten.

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Author's address: R. A. POWELL, Department of Zoology, North Carolina State University, Raleigh, N.C. 77650, U.S.A.